Running title: CAM plant stomata

Jamie Males, jom23@cam.ac.uk

Update Article

Stomatal biology of CAM plants

Jamie Males[1] & Howard Griffiths[1]

[1] Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EA, United Kingdom

* Author for correspondence

One-sentence summary

Recent advances in the stomatal biology of CAM plants are reviewed and key opportunities for future progress are identified.

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Corresponding author email
jom23@cam.ac.uk (JM)

Abstract

Crassulacean acid metabolism (CAM) is a major physiological syndrome that has evolved independently in numerous land plant lineages. CAM plants are of great ecological significance and increasing interest for their water-use efficiency and drought resistance. Integral to the improvement in water-use efficiency that CAM affords is a unique pattern of stomatal conductance, distinguished by primarily nocturnal opening and often extensive diurnal flexibility in response to environmental factors. Here we assess how recent research has shed new light on the functional biology of CAM plant stomata, and integration within the broader physiology and ecology of succulent organisms. Divergences in stomatal sensitivity to environmental and endogenous factors relative to C_3 species has been a key aspect of the evolution of functional CAM. Stomatal traits of CAM plants are closely coordinated with other leaf functional traits, and structural specialisation of CAM stomatal complexes may be of undiagnosed functional relevance. We also highlight how salient results from ongoing work on C_3 plant stomatal biology could apply to CAM species. Key questions remaining relate to the interdependence between stomatal and mesophyll responses, and are particularly relevant for bioengineering of CAM traits or bioenergy crops to exploit enhanced water-use efficiency and productivity on marginal land. With the increasing availability of powerful analytical tools and the emergence of new model systems for the study of the molecular basis of physiological traits in CAM plants, many exciting avenues for future research are open to intrepid investigators.

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Corresponding author email
jom23@cam.ac.uk (JM)

Introduction

CAM is a celebrated example of a convergent physiological syndrome (i.e. a characteristic combination of traits), having evolved independently on numerous occasions across the land plants (Smith & Winter, 1996). Furthermore, thanks in part to their ability to withstand multiple, synergistic stressors (Lüttge, 2010), CAM plants have successfully invaded diverse environmental spaces ranging from deserts to cloud forests. In many tropical and subtropical vegetation types CAM is a dominant ecophysiological syndrome, and CAM plants represents at least 6% of higher plant species richness (Dodd et al., 2002).

The physiological mechanisms and ecological significance of the gas exchange rhythms of plants performing crassulacean acid metabolism (CAM) have been the subject of curiosity and investigation for not just decades, but centuries (de Saussure, 1804; Heyne, 1815; Osmond, 1978; Ting, 1987; Faak, 2000). The quintessential feature of CAM is nocturnal primary carbon assimilation by the enzyme phospho-*enol*-pyruvate carboxylase (PEPC), producing malic acid which is stored in mesophyll cell vacuoles and subsequently decarboxylated during the light period to provide CO_2 for refixation by RuBisCO (Winter & Smith, 1996). While a few lineages are capable of performing CAM in tissues lacking stomata, including some aquatic plants with leaves with no stomata ('astomatous'; Keeley, 1998) and epiphytic orchids with astomatous chlorophyllous roots (Goh et al., 1983), in most cases CAM involves the delivery of CO_2 to the mesophyll via stomata that are open in the dark (Winter & Smith, 1996). Non-negligible nocturnal stomatal conductance is increasingly recognised as an important physiological phenomenon in many C_3 plants (Zeppel et al., 2012; de Dios et al., 2013; Forster, 2014; Matimati et al., 2014; Zeppel et al., 2014; Cirelli et al., 2015; de Dios et al., 2016), but stomata of CAM plants displaying primarily nocturnal CO_2 assimilation clearly must differ from those of C_3 plants in their responsiveness to environmental and endogenous stimuli.

The global CAM flora combines great ecological diversity with a wide variety of evolutionary backgrounds, and comparative studies of variation in the stomatal biology of different CAM lineages allows two overarching questions to be distilled. First, what characteristics unite the functional biology of CAM plant stomata? Were there multiple evolutionary routes to the same phenomenology, or do all CAM plants share the same molecular and metabolic basis for stomatal behaviour? Secondly, how does variation in stomatal form and function among CAM species

98 underpin physiological adaptation to the wide range of environmental niches these plants have
99 come to occupy?

100 Researchers have adopted a multiplicity of approaches to shed light on these questions, spurred
101 both by the enduring appeal of CAM as a 'curiosity' (Osmond, 1978), and the rapidly-growing
102 interest in the application and engineering of CAM plants for bioenergy production (Borland et al.,
103 2011, 2014, 2015; Owen & Griffiths, 2014; DePaoli et al., 2014; Yang et al., 2015). Simultaneously,
104 the wider field of stomatal biology has experienced a renaissance in recent years, with numerous
105 advances being made through both empirical and theoretical work. Although this research has
106 generally been carried out in a C_3 context, lessons can be carried through to the CAM world. Here we
107 provide a general synthesis of current understanding of CAM stomatal biology, and identify key
108 opportunities for future research.

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Advances Box

- Transcriptomic analyses have begun to shed light on the regulation of stomatal rhythm in CAM plants
- Facultative CAM species are attracting attention as tractable systems for exploring the genetic basis of CAM stomatal biology
- Emerging analytical methodologies are providing fresh insights into the sensitivity of stomata to endogenous and exogenous stimuli

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112 **Patterns of stomatal conductance**

113 The four classical phases of CAM, driven by changes in carbon metabolism, coincide with changes in
114 stomatal conductance across the diurnal cycle (Fig. 1; Osmond, 1978). Stomatal conductance is
115 typically highest during the dark period (Phase I), in association with nocturnal CO_2 assimilation by
116 PEPC. During the dark period, mesophyll factors are often more important in limiting the rate of
117 nocturnal assimilation than is stomatal conductance (Winter, 1985; Winter et al., 1985). Around
118 dawn, there is often a spike in stomatal conductance and some direct fixation of CO_2 by RuBisCO
119 (Phase II), which continues to fix CO_2 released by decarboxylation of malic acid behind closed
120 stomata during most of the light period (Phase III). During the late afternoon, if environmental
121 conditions are favourable there may be a period of stomatal opening with direct RuBisCO-mediated

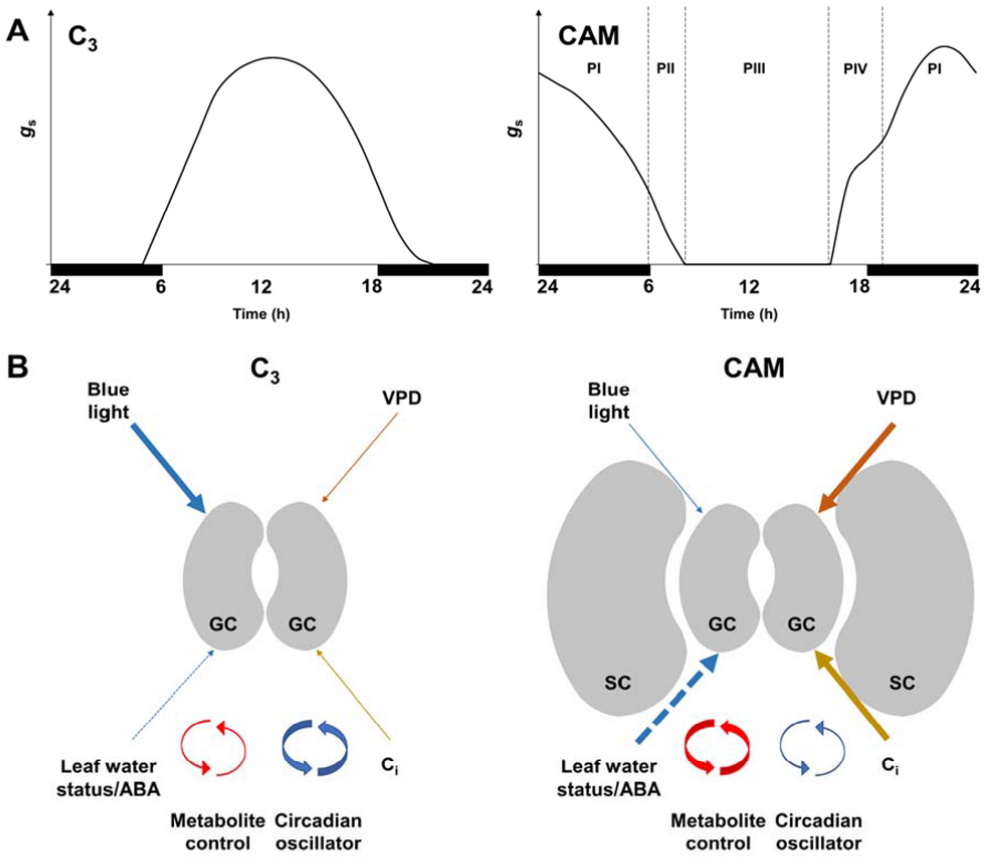

Figure 1. Summary of differences in stomatal biology of C_3 and CAM plants.

(A) *Representative curves of day/night rhythms in stomatal conductance (g_s) in C_3 and CAM plants.* The Phases of the classical CAM gas exchange rhythm (Phases I-IV *sensu* Osmond, 1978) are displayed.

(B) *Schematic comparison of factors affecting regulation of stomatal aperture in C_3 and CAM plants.* Thicknesses of arrows indicate relative importance of factors in typical species of either photosynthetic pathway. The response of guard cells (GC) to blue light appears to be weaker or absent in many CAM species (e.g. Tallman et al., 1997), while strong sensitivity to leaf-air vapour pressure deficit (VPD) occurs in many CAM plants (e.g. Lange & Medina, 1979). Leaf (or whole-plant) water status, often acting on stomatal aperture in an ABA-dependent manner, may have a stronger effect in CAM species (Jewer et al., 1981). Intercellular CO_2 concentration (C_i) is a key driver of stomatal rhythms in CAM plants (e.g. Wyka et al., 2005), and this is intimately linked to the importance of metabolite control in CAM (Dever et al., 2015). While the circadian oscillator still plays a role in shaping CAM stomatal rhythms (von Caemmerer & Griffiths, 2009), it is perhaps of less direct importance than in C_3 plants. Structural modifications are common in stomata of both C_3 and CAM species, but specialised stomatal complex morphologies with large subsidiary cells appear to be overrepresented among CAM plants (see section "Stomatal structure-function relationships").

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fixation of CO_2 (Phase IV). However, this canonical pattern of gas exchange is subject to a large amount of interspecific, intraspecific, and intra-individual variation. One of the most remarkable features of CAM is its plasticity in response to environmental variability. The expression of the classical phases of CAM is modulated in response to recent and current environmental conditions

(Dodd et al., 2002; Owen & Griffiths, 2013). Under low water availability and high evaporative demand, for instance, Phase IV stomatal opening may be completely abolished.

Additionally, two frequently observed modes of CAM do not conform to the textbook four-phase gas exchange profile: "CAM cycling" and "CAM idling" (Sipes & Ting, 1985). CAM cycling involves the nocturnal operation of respiratory recycling and diurnal stomatal opening for direct RuBisCO-mediated assimilation, and most often occurs as a facultative trait in C_3-CAM or "weak CAM" species (Silvera et al., 2010). Meanwhile under CAM idling, stomata remain closed throughout the day and night, with a proportion of respiratory CO_2 being refixed. CAM idling is often induced under extreme seasonal drought stress in "strong CAM" species, maximising water retention (Silvera et al., 2010). This capacity for close environmental tracking on both diurnal and seasonal bases maximises integrated water-use efficiency and is therefore an important contributor to the ecological success of CAM plants in stressful habitats.

[FIGURE 1]

Stomatal sensitivity to endogenous stimuli: control of, and by, CAM

Stomata and mesophyll cell processes may be controlled by distinct circadian clocks in C_3 species (Hubbard & Webb, 2016), and understanding the interplay between these cycles could provide insights for the co-ordination of CAM, as well as the interplay between responses to internal and external signals via metabolite feedback, internal CO_2 availability (C_i), and environmental cues (Fig. 1).

The circadian rhythm of CAM plants involves the same system of clock genes as have been intensively studied in *Arabidopsis* (Boxall et al., 2005; Hubbard & Webb, 2016), and control diurnal oscillations in physiological processes including photosynthetic enzyme activity (Nimmo, 2000; Hartwell, 2005). However, there is evidence for an important role for metabolite control of the temporal dynamics of the CAM cycle. For instance, manipulation of key decarboxylation and metabolite regeneration processes in *Kalanchoë fedtschenkoi* had a direct disruptive effect on the mesophyll circadian clock (Dever et al., 2015). Furthermore, reducing the capacity of CAM leaves to synthesize malic acid at night (by removal of external CO_2 supply) showed that associated reductions in metabolite concentrations could override circadian control of PEPC kinase (Borland et al., 1999). However, the extent that the guard-cell circadian cycle is synchronised with, or driven by, the mesophyll CAM cycle, remains to be determined.

Additional insights have been gained from combined measurements of gas exchange and

carboxylation enzyme co-regulation under continuous light. In *Mesembryanthemum crystallinum*, the timing of circadian rhythms of both stomatal conductance, CO_2 assimilation and Rubisco/PEPc continued to be synchronised across light and dark cycles (Davies & Griffiths, 2012). However, stomatal conductance was lower when Rubisco carboxylation predominated at the end of the light period, and higher when PEPC carboxylation predominated at the end of the dark periods, perhaps suggesting that guard cells are responding to the extent of CO_2 drawdown and intercellular CO_2 concentration (C_i; Davies & Griffiths, 2012).

Sensing CO_2 concentrations has long been implicated in both C_3 and CAM stomatal movements, and intuitively, responding to C_i would seem to be the signal most likely to regulate the inverse stomatal cycle associated with CAM. At the beginning of Phase I of CAM, stomatal opening is thought to be driven by reduced C_i when PEPC activity increases at dusk (Wyka et al., 2005; Griffiths et al, 2007; von Caemmerer & Griffiths, 2009). In the morning, stomatal closure is then reinforced by the decarboxylation of stored malate during Phase III. This, coupled with respiration, can cause C_i to increase up to 100 times atmospheric concentration (Cockburn et al., 1979; Spalding et al., 1979). The reopening of stomata to initiate Phase IV is associated with the end of malic acid breakdown and hence internal CO_2 limitation.

The responsiveness of CAM stomata to changing ambient CO_2 transients was investigated in relation to degree of leaf succulence and commitment to the CAM cycle (von Caemmerer & Griffiths, 2009). The stomata of the more succulent *K. daigremontiana* were more responsive to a CO_2 transient reduction at night, whereas stomata in the less succulent *K. pinnata* were more responsive during daytime Phase IV gas exchange. When CO_2 uptake and malic accumulation were reduced overnight, and subsequent C_i regeneration lowered during Phase III, stomata still closed and showed little instantaneous response to CO_2 transients, suggesting that circadian control of stomata remains a key factor controlling the CAM cycle in both species (von Caemmerer & Griffiths, 2009). However, there is still a lack of clarity in defining the interplay between circadian inputs from guard cells and mesophyll metabolism, and how sensing of C_i and metabolites are transduced by stomata in CAM plants. The major advances in our understanding of the mechanism of CO_2 sensing and regulation of stomatal conductance in C_3 plants (Chater et al., 2015; Engineer et al., 2016), provide an excellent springboard for exploration of the role of equivalent genetic systems in CAM species. Abraham et al. (2016) have already demonstrated that there is a concerted shift in the temporal expression of components of CO_2 signalling pathways in the constitutive CAM species *Agave americana* relative to C_3 Arabidopsis. The generality of this observation among other CAM systems should now be explored, and the regulatory mechanisms further elucidated.

Stomatal responses to external stimuli

In addition to circadian control of stomatal and mesophyll processes, environmental tracking by CAM plant stomata is mediated by the integration of endogenous and exogenous signals by guard cells, as in C_3 species (Assmann & Jegla, 2016).

The role of blue light in the stomatal movements of CAM plants has also not been fully resolved (Inoue & Kinshita, 2017). While there is some evidence for the involvement of blue light signalling in the regulation of stomatal conductance and malate decarboxylation in CAM bromeliads (Ceusters et al., 2014) and for the induction of CAM in *Clusia minor* (Grams and Thiel, 2002), other studies performed with facultative CAM plants have concluded that blue light regulates stomatal conductance of these plants only when they are in the C_3 mode (Lee & Assmann, 1992; Tallman et al., 1997). Moreover, the results of transcriptomic analysis of the constitutive CAM plant *Agave americana* were not consistent with a role for stomatal regulation by blue light (Abraham et al., 2016). This apparent divergence in stomatal regulation in different CAM lineages could hint at the existence of multiple mechanistic routes to CAM-like stomatal function.

Both leaf water potential and the humidity of the leaf microenvironment also affect stomatal conductance. Declining leaf water potential is a powerful driver of stomatal closure in C_3 plants (Rodriguez-Dominguez et al., 2016). Although comparative data are quite limited, succulent CAM plant stomata tend to close at much higher (less negative) water potentials than those of co-occurring C_3 plants (Osmond, 1978), consistent with evidence that succulent plants tend to avoid, or be isolated from, drought stress (Nobel, 1988; Males & Griffiths, in review). Complete stomatal closure can therefore occur throughout both the light and dark periods (CAM idling).

Malate has been proposed as a mesophyll to guard cell signal in the regulation of stomatal aperture in response to mesophyll turgor and light-dark transitions in C_3 plants (Araújo et al., 2011; Lawson et al., 2014; Costa et al., 2015), while oxaloacetate has been shown to be an effective inhibitor of guard cell anion channel activity (Wang & Blatt, 2011). The involvement of organic anions in stomatal regulation has interesting implications for CAM plants, in which malate can accumulate to high concentrations during Phase I (Osmond, 1978). The importance of abscisic acid (ABA), which is synthesised and mobilised in roots and shoots in response to declining water potential, in regulating stomatal closure in CAM plants, as compared to C_3 plants, remains to be determined (Cutler, 2017; Jezek & Blatt, 2017). Jewer et al. (1981) suggested that stomata of CAM plants might be hypersensitive to ABA, which would be consistent with strategies for avoiding soil water deficits

(tissue water potentials usually > -1 MPa), water storage and rapid recharge in succulent tissues. Recent progress in our understanding of the role of ABA in the evolution of stomatal responses should be brought to bear on CAM plants (Negin & Moshelion, 2016), and the debate over the origins of signalling pathways for both ABA and CO_2, and contrasting observations in ferns (which do contain CAM lineages: Ong et al., 1986; Winter et al., 1986) remain to be determined (McAdam & Brodribb, 2012; c.f. Chater et al., 2015; Franks & Britton-Harper, 2016).

An apparent feedforward response of transpiration to rising leaf-air vapour pressure deficit (VPD), in which stomata seem to respond directly to humidity rather than indirectly via leaf water status, has been observed in some CAM lineages, with important consequences for assimilation rates and water-use efficiency under contrasting humidity regimes (Lange & Medina, 1979; Osmond et al., 1979; Martin & Siedow, 1981; Von Willert et al., 1985; Lüttge et al., 1986; Herppich, 1997). Epiphytic CAM species might be expected to show particularly high levels of stomatal sensitivity to VPD, given the special adaptive value this would have in highly water-limited epiphytic environments (see discussion of integrated leaf traits below). Indeed, in C_3 plants, stomatal sensitivities to VPD and leaf water potential are often strongly correlated with leaf or petiole hydraulic conductances and their sensitivity to tissue water potential (Brodribb & Jordan, 2008; Ocheltree et al., 2013, 2014; Klein, 2014; Tombesi et al., 2014; Bartlett et al., 2016). The mechanisms underlying stomatal sensitivity to VPD remain a controversial and active area of research, with the possibility of liquid- and/or vapour-phase signals being involved alongside ABA synthesis and signalling within guard cells (Peak & Mott, 2011; Bauer et al., 2013; Buckley & Mott, 2013; Mott & Peak, 2013; McAdam et al., 2016). Because of the potentially significant metabolic and signalling interactions between guard cells and the mesophyll, integrated investigation of stomatal sensitivity and the dynamic responses of the critical extra-vascular component of leaf hydraulic conductance in CAM (and C_3) species is highly desirable (Sack et al., 2016; Trifiló et al., 2016). Analysis of the spatiotemporally dynamic expression patterns of aquaporins and of possible interactions between stomatal physiology and mesophyll osmotic properties could be especially fruitful (Pou et al., 2013; Martorell et al., 2015).

A final factor that has been demonstrated to influence stomatal conductance in CAM plants is temperature, with optimal CAM activity usually associated with narrow and relatively low (usually ~15-25°C) nocturnal temperature windows (Yamori et al., 2014). Both thermoperiodic effects (Ting et al., 1967) and instantaneous leaf temperature effects (Nobel & Hartsock, 1979) have been reported. Given the known importance of nocturnal leaf temperature for the efficiency of malate synthesis and decarboxylation (e.g. Neales, 1973; Moradshahi et al., 1977; Nobel & Hartsock, 1984), water-use efficiency should be maximised through the regulation of stomatal conductance in line with temperature.

Guard cell metabolism

Guard cell metabolism in C_3, C_4 and CAM plants continues to be a fast-paced area of research with many critical questions awaiting resolution (Daloso et al., 2016; Santelia & Lunn, 2017). The similarities between guard cell metabolism in C_3 plants and the metabolism of mesophyll cells of CAM plants are striking, which led Cockburn (1981) to suggest that a transfer of guard cell-like metabolism to mesophyll cells was a central event in evolutionary origins of CAM. More recent work has highlighted the importance of organic acids in C_3 guard cell function (e.g. Wang & Blatt, 2011; Penfield et al., 2012; Daloso et al., 2015; Medeiros et al., 2016).

Controlled ion fluxes are fundamental to the operation of stomatal movements (Chen et al., 2012; Minguet-Parramona et al., 2016; Eisenach & De Angeli, 2017; Jezek & Blatt, 2017). In comparing the day-night transcriptomic profiles of C_3 Arabidopsis and the constitutive CAM plant *Agave americana*, Abraham et al. (2016) showed that there was a coordinated shift in the temporal expression patterns of key ion channels in *A. americana*. Notably, orthologous vacuolar chloride channel genes displayed reciprocal expression in the C_3 and CAM species, which could help to drive appropriate charge balancing.

The presence of RuBisCO in the guard cells of some CAM plants needs further investigation in the context of the emerging role of guard cell photosynthesis in the regulation of stomatal conductance in C_3 plants (Madavhan & Smith, 1982; Azoulay-Shemer et al., 2015). Tallman (2004) suggested that guard cell photosynthesis could be supplied with large amounts of CO_2 from the mesophyll during Phase III of CAM, establishing a strong sink for NADPH and thus inhibiting the degradation of guard cell endogenous ABA, which promotes stomata closure (Lind et al., 2015). In this way, guard cell photosynthesis in CAM plants could assist in the maintenance of negligible diurnal stomatal conductance during the light period.

Santelia & Lawson (2016), citing earlier work carried out by Pantoja & Smith (2002), recently highlighted the absence of the correlation between malate currents across the guard cell tonoplast and cytosolic calcium concentrations across CAM species that would be expected if they shared a uniform regulatory mechanism. This apparent diversity in stomatal physiology could have important consequences for our understanding of the evolution of complex syndromes like CAM. Further empirical studies of this topic are needed to advance our understanding of the imposition of daytime stomatal closure in CAM plants. Cell-specific perturbation of metabolic function offers an exciting opportunity in this respect (Lawson et al., 2014).

Coordination of stomatal traits with leaf trait networks

CAM species have rarely been included in analyses of leaf economic trait variation, partly because succulence is one trait which uncouples leaf-mass based relationships (Grubb et al., 2015; Males & Griffiths, in review). However, in a survey of leaf economic, anatomical and hydraulic traits in the Bromeliaceae, we found that CAM bromeliads tended to show lower stomatal density and conductance as well as lower leaf hydraulic conductance, photosynthetic capacity and nutrient content, and higher leaf mass per unit area (Males & Griffiths, in review). Variation in stomatal traits appears to be accommodated within a network of coordinated leaf traits in CAM species in the same way as has been observed in C_3 plants (Reich et al., 1997, 1999; Wright et al., 2004, 2005; Donovan et al., 2011; Vasseur et al., 2012; Díaz et al., 2016). Recent modelling and empirical studies have highlighted the importance of the alignment of variation in stomatal, xylem and veinal traits in angiosperms for optimal physiological function (Brodribb et al., 2013, 2016; Fiorin et al., 2016; Murphy et al., 2016; Scoffoni et al., 2016). It would be particularly interesting to explore the degree of coordination between Phase I (night-time) and Phase IV (daytime) stomatal and mesophyll conductances in CAM plants. Although few data are available, it is expected that mesophyll conductance is generally low in CAM plants due to their succulent anatomy with tight cell-packing (Maxwell et al., 1997; Nelson & Sage, 2008). Campany et al. (2016) recently showed that coupled responses of stomatal and mesophyll conductances to light improved carbon gain during sunfleck events in shade leaves of a *Eucalyptus* species. Similar effects are likely to be important in CAM epiphytes of the humid tropics with sunfleck-driven carbon economies.

Stomatal structure-function relationships

CAM has arisen in a wide range of taxonomic and morpho-anatomical backgrounds, and this is reflected in the various stomatal complex morphologies found in different CAM lineages. When variation is considered among the angiosperms at the family level, using the APG IV classification (The Angiosperm Phylogeny Group, 2016) and anatomical data from the DELTA database (Watson & Dallwitz, 1992), the proportional occurrence of different stomatal complex morphologies shows several potentially important differences between CAM and C_3 lineages. None of the monocot families with CAM elements display anomocytic stomata (lacking subsidiary cells), whereas 26% of exclusively C_3 monocot families do. Tetracytic stomata (four subsidiary cells) are nearly twice as common in CAM families as in C_3 families. Among the dicots, anomocytic stomata are also less

common in CAM families, and there are relatively more CAM families with paracytic stomata (two subsidiary cells). The overrepresentation of CAM in families with more specialised stomatal complexes in both monocots and dicots has not been investigated from a functional perspective. However, it is well-established that the presence of subsidiary cells in C_3 and C_4 species can enhance the kinetics of stomatal movements (Franks & Farquhar, 2007), and systematic differences in stomatal kinetics and sensitivity may occur between CAM species with contrasting stomatal morphologies. Empirical and theoretical work in the C_3 context also suggests that stomatal size could be an important determinant of the rapidity of stomatal movements (Drake et al., 2013; Lawson & Blatt, 2014; Raven, 2014), although this relationship may be modulated by guard cell morphology (McAusland et al., 2016). These trait linkages are potentially of great evolutionary and ecological importance, and could easily be tested for in CAM plants. It is interesting to note that among the few fern lineages to have evolved CAM, modified polocytic and pericytic stomatal complexes occur, wherein the guard cell pair is surrounded either completely or partially by one or two subsidiary cells (e.g. Patel et al., 1975; Sen & Hennipman, 1981).

When compared with their nearest C_3 relatives, CAM lineages show no consistent differences in guard cell ultrastructure (Faraday et al., 1982), but do tend to display a shift towards lower stomatal densities and lower maximal conductances in CAM plants (Ting et al., 1972; Kluge & Ting, 1978; Gibson, 1982; Zambrano et al., 2014; Males & Griffiths, in review). These reductions have widely been interpreted as adaptive xeromorphic traits in their own right, but there is now accumulating evidence for a developmental constraint that generates a robust negative relationship between stomatal density and the sizes of guard cells and mesophyll cells (Brodribb et al., 2013). Since CAM is dependent on the presence of highly-vacuolate succulent cells for malate storage, low stomatal densities could be a necessary trade-off. Further investigation of the coordination of stomatal traits, cell sizes, succulence and perhaps genome sizes (Beaulieu et al., 2008) could prove illuminating.

Stomata on the rugged CAM adaptive landscape

CAM is now often discussed as a continuum of intergrading and flexible photosynthetic modes rather than a monolithic, discrete trait (Silvera et al., 2010; Winter et al., 2015). The existence of a wide range of CAM types and the occurrence of evolutionary reversions from CAM to C_3 (Teeri, 1982a,b; Silvera et al., 2009; Givnish et al., 2014) is a reflection of a rugged adaptive landscape with multiple peaks. While the description of the C_3-C_4 adaptive landscape as 'Mount Fuji-like' (Heckmann et al., 2013) is a simplified abstraction, there are convincing accounts of the demonstrable increases in fitness associated with each step between full-C_3 and full-C_4 metabolism in independent C_4 origins

(Christin et al., 2011, 2013; Griffiths et al., 2013; Heckmann et al., 2013; Sage et al., 2013; Schlüter & Weber, 2016). In the absence of the wealth of phylogenetic and physiological information enjoyed by the C_4 community, and despite the possibility that C_4 and CAM represent alternative evolutionary pathways from similar starting points (Edwards & Ogburn, 2012), the picture for CAM is far murkier (Hancock & Edwards, 2014). Succulence has been identified as an anatomical prerequisite for CAM (Sage, 2002; Zambrano et al., 2014; Heyduk et al., 2016), but beyond this there is little clarity regarding the relative timing of the acquisition of component traits of the CAM syndrome, or the extent to which different types of CAM could represent independent adaptive peaks. In particular, the involvement of stomatal innovation in convergent origins of CAM is unclear. How does the capacity for stomatal flexibility vary among CAM lineages' C_3 sister taxa? During evolutionary transitions from C_3 to CAM, do any less obvious changes in stomatal biology occur prior to the appearance of the inverse stomatal rhythm? Is the answer to this question the same for lineages that have only evolved weak CAM (CAM cycling) as for those that have evolved strong CAM? Concerted efforts to improve phylogenetic resolution in critical lineages in which C_3-to-CAM transitions have occurred, more accurate diagnosis of "cryptic" low-level CAM, and targeted surveys of stomatal physiological traits and molecular biology in representative taxa would all be important preliminary steps towards unravelling these longstanding evolutionary puzzles.

Conclusions and Future Perspectives

CAM is a major ecophysiological syndrome that has been repeatedly identified as providing high potential for sustainable production under climate change (Borland et al., 2011, 2014, 2015; Owen and Griffiths, 2014; Yang et al., 2015). Harnessing this potential is contingent upon a comprehensive understanding of the underlying physiology of CAM. Recent work has contributed to our knowledge of how stomatal specialisation is involved in the unique metabolic flexibility and water-use efficiency afforded by CAM, while insights gained from work on the stomatal biology of non-CAM plants can also be reinterpreted from a CAM perspective. However, there is still much to be learned about the functioning of CAM stomata (see Outstanding Questions Box). One promising route for future research will be to make use of known C_3-CAM intermediates and facultative CAM species as tools for exploring the molecular changes associated with the commencement of CAM stomatal rhythms (Winter & Holtum, 2014; Brilhaus et al., 2016). The identification of gradients in the relative contributions of C_3 and CAM along the linear leaves of C_3-CAM intermediate monocot species is another naturally-occurring system ripe for further investigation (Popp et al., 2003; Freschi et al., 2010). Increasingly sensitive technologies will improve the ease of *in situ* and *ex situ* physiological

characterisation (e.g. Barla & Rhodes, 2016), and robust transcriptomic methodologies will be crucial for elucidating the molecular genetic basis of divergences in stomatal function along the CAM continuum and under variable environments. Finally, the integration of recently developed physiological models of CAM (Owen & Griffiths, 2013; Bartlett et al., 2014; Hartzell et al., 2015) with more detailed models of stomatal conductance could be a powerful way of exploring the significance of variation in stomatal traits for carbon gain and water-use efficiency.

Outstanding Questions Box

- How does structural diversity impact on stomatal function in CAM plants? How does this affect assimilation rates and water-use efficiency?
    - *Characterisation of stomatal morphology and visualisation of responses to stimuli*
    - *Biophysical modelling of relationships between stomatal movements and conductance*
    - *Quantitative comparison of stomatal and mesophyll limitations of assimilation and water-use efficiency*

- How do stomatal kinetics sensitivities to endogenous and exogenous factors vary among CAM plants? Are there consistent differences in sensitivity between CAM species and their C_3 relatives?
    - *Accurate resolution of phylogenetic relationships within CAM clades and C_3 sister taxa*
    - *Characterisation of stomatal sensitivities and kinetics for representative lineages*
    - *Define the interplay between circadian control of guard cell and mesophyll cell metabolism, and associated sensing and signalling systems*

- Can models of stomatal physiology be reconciled with models of CAM physiology?
    - *Incorporation of expanded stomatal circuit into systems dynamics models of CAM*
- What are the molecular determinants of the stomatal rhythms of CAM plants?
    - *Comparative –omics studies of constitutive CAM plants and pre- and post-induction facultative CAM plants*
    - *Functional genetic characterisation in model systems (e.g.* Kalanchoë*)*

- Do CAM stomatal rhythms need to be engineered into C_3 species?
    - *Application of transgenic and emerging genome editing techniques to manipulate C_3 stomatal signalling and/or mesophyll processes*

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